Growth, maximum daily ration and intraspecific cohabitation of the moray *Gymnothorax polyuranodon* (Muraenidae) in a freshwater aquarium

by

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Abstract. – Some predominantly marine fish families include a small proportion of species that are obligate freshwater inhabitants, and there is accumulating evidence for obligate freshwater species within the family Muraenidae. Whether the muraenid *Gymnothorax polyuranodon* (Bleeker, 1854) can survive, grow and coexist over an extended period in captive freshwater conditions was tested following repeated observations of this species in freshwater streams of the Australian Wet Tropics. Changes in the body size of four individuals held in a 1200 litre freshwater aquarium revealed that yearly growth ranged from a minimum of 21.0 cm total length (TL) and 2.4 times body mass to 26.5 cm TL and 3.9 times body mass. Maximum daily ration of individuals (fed worms, prawns and fish) ranged from 3.4% to 3.9% of body mass. Individuals coexisted peacefully, with only brief bouts of intraspecific aggression that included biting. While the full life cycle of *G. polyuranodon* remains unresolved, the current study reinforces field observations and microchemistry insights indicating that this species can occupy and grow in freshwater ecosystems, and points toward the likelihood that the species probably plays an important and previously unrecognised mesopredatory role.

Résumé. – Croissance, ration alimentaire journalière maximale et cohabitation intraspécifique de la murène *Gymnothorax polyuranodon* (Muraenidae) dans un aquarium d'eau douce.

Certaines familles de poissons majoritairement marines possèdent une petite proportion d'espèces qui sont strictement d'eau douce. C'est le cas de la famille des Muraenidae pour laquelle il y a de plus en plus de preuves de l'existence d'espèces d'eau douce. La capacité de *Gymnothorax polyuranodon* (Bleeker, 1854) à survivre, grandir et coexister sur une longue période dans des aquariums d'eau douce a été testée suite à de multiples observations de cette espèce dans des rivières d'Australie tropicale. Le taux de croissance annuel de quatre individus maintenus dans un aquarium d'eau douce de 1200 litres varie de 21,0 cm à 26,5 cm en longueur totale (LT) et le poids augmente de 2,4 à 3,9 fois. La ration de nourriture journalière maximale des individus (vers, crevettes et poissons) a varié de 3,4 à 3,9% du poids corporel. Les individus ont coexisté pacifiquement, avec de rares événements d'agressions, comme les morsures. Alors que la totalité du cycle de vie de *G. polyuranodon* n'est pas encore connu, cette étude renforce les observations faites sur le terrain et les éléments apportés par les microanalyses chimiques qui indiquent que cette espèce peut vivre et grandir en eau douce. Cette étude montre que cette espèce a probablement un rôle important et encore non reconnu dans la mésoprédation.

A number of predominantly marine teleost and elasmobranch families comprise a small proportion of obligate freshwater species or populations. Among the teleosts, examples include, but are by no means restricted to, the Soleidae, Cynoglossidae, Syngnathidae, Blenniidae, Engraulidae, Tetraodontidae; and elasmobranch examples include the Pristidae and Dasyatidae (Allen *et al.*, 2002; Lovejoy *et al.*, 2006; Nelson, 2006; Blanco-Garrido *et al.*, 2009). There are also some families comprised entirely or mostly of obligate freshwater species, which have radiated from distant marine ancestors (*e.g.* Potamotrygonidae, Terapontidae) (Allen *et al.,* 2002; Lovejoy *et al.,* 2006; Davis *et al.,* 2012). The evolution, biogeography, ecology and physiology of these fishes are all fascinating areas of study, and discovering anomalous freshwater species within an otherwise exclusively marine phylogeny is an exciting prospect.

Morays, family Muraenidae, are a predominantly marine group of teleosts comprising in the order of 200 species (Allen *et al.*, 2002; Nelson, 2006) and include a few species recorded from brackish and freshwater ecosystems (Pinto, 1987; Böhlke and McCosker, 2001; Allen *et al.*, 2002; Monkes, 2006; Ebner *et al.*, 2011). The family includes numerous species that presumably represent important predators in marine reef ecosystems (*e.g.* Hiatt and Strasburg, 1960) but their cryptic and stealthy behaviour renders them somewhat difficult to study. The Freshwater moray, *Gymnothorax polyuranodon* (Bleeker, 1854) has only been observed in rivers and is widely distributed in the tropical Indo-Pacific region, where it is occasionally encountered and is probably

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best considered an elusive species (Weber and de Beaufort, 1916; Kottelat *et al*., 1993; Marquet *et al*., 2003; Ebner *et al*., 2011). Ebner *et al*. (2011) gathered and examined records of *G. polyuranodon* from North-eastern Australia. In that study, all but one of the 36 records were found to correspond with freshwater or mildly brackish conditions up to salinity of 4, and the remaining record was of an elver from an estuary, indicating that the adult-phase of this species is associated with tropical rivers. More recently, Tsukamoto *et al*. (2014) used otolith microchemistry to demonstrate that juveniles and/or small-bodied adult specimens (275-344 mm TL) had occupied freshwater and likely have a catadromous life cycle. However, the life history and ecology of this species needs further investigation; no studies on the larvae have been documented and the adult phase may simply be more easily detected in fresh rather than estuarine or marine habitats. In reality, an understanding of the ecology of this species is compromised by its inherent rarity. One means of partially overcoming this situation is to bring a small number of individuals into captivity for observation.

The primary aim of the current study was to test the hypothesis that *G. polyuranodon* could grow and survive in freshwater for an extended period. A secondary aim was to develop an understanding of the biology of the species and specifically aspects of feeding biology and intraspecific interaction. Morays are mostly solitary and can be aggressive and even cannibalistic (Young and Winn, 2003; Purser, 2005). If they are to be kept together in captivity, Purser (2005) recommends a strategy that includes: choosing similar sized individuals of a single docile species, providing multiple refuge holes in a large aquarium and regular feeding to minimise aggression and cannibalism. Since adult *G. polyuranodon* have a small head relative to body size and possess small-teeth, cannibalism is unlikely in this species (except where large discrepancies in body size occur). After observations of a number of individuals in close proximity in the wild, this species was chosen as a good candidate for coexistence in captivity. Therefore, a third aim of this study was to investigate intraspecific interactions of *G. polyuranodon* over an extended period in captivity.

METHODS

Field collection and aquarium conditions

In December 2009, *G. polyuranodon* (n = 4) was collected by dip net from the lower freshwater reaches of Noah Creek (altitude ~0 m above sea level (ASL)), near Cape Tribulation, Australia 16°08'31"S, 145°25'44"E (Fig. 1A). Individuals were transported to a 470 L (L × W × H = 1.83 × 0.46 × 0.60 m) freshwater aquarium in Mareeba (altitude ~400 m ASL), which provided shelter in the form of logs, rocks, plastic pipes and ribbonweed (*Valliseneria* spp.) and partial fluorescent lighting to provide darkened refuge areas. Individuals were offered a range of food items for several weeks before feeding commenced (time until first feed was 26, 28, 28, 29 days for the four individuals). Once all four individuals were feeding regularly for at least one week, they were fasted for 48 hours to minimise varying gut fullness and avoid biasing mass estimates, then weighed (± 1 g) and measured (total length ± 5 mm) under anaesthesia (0.1 ml AQUI-S® per litre). Individuals were then transferred to a 1200 L (L × W × H = 3.0 × 0.6 × 0.7 m) freshwater aquarium under similar habitat and lighting conditions to that of the previous aquarium (Fig. 1B, Fig. 2). Un-fluoridated water was sourced from the Mareeba domestic supply (Tab. I). Approximately one-third of the aquarium water was changed fortnightly (without adding de-chlorinating chemicals) and more frequently in relation to heavy feeding periods to maintain adequate water quality (see Graynoth and Taylor, 2000). No salt or medicinal chemicals were added to the water during the study period.

Growth trial

Over a one-year period individuals were fed opportunistically; to partial or full satiation once daily for three to five consecutive days interspersed with a once-weekly feeding for two to three weeks. The stable food items offered throughout the study were defrosted, precooked and raw marine prawns and defrosted fish (Western Australian Whitebait, *Hyperlophus vittatus*) (Fig. 1G, I). Additionally, live garden worms (Fig. 1H) or live freshwater prawns (*Macrobrachium* spp.) were occasionally used to supplement the diet. Small native freshwater fishes (*Melanotaenia splendida*, *Cairnsichthys rhombosomoides, Hypseleotris compressa, Craterocephalus stercusmuscarum, Glossogobius illimis*) were often living sympatrically in the aquarium but were rarely consumed by *G. polyuranodon*. Uneaten food was removed from the aquarium within two hours of being offered. Interactions among individuals were observed and noted throughout the study. Photographs were taken of some of these interactions and of temporary wounds resulting from biting.

In an effort to mimic wild stream conditions, the aquarium was not artificially heated. Average monthly water temperature was calculated from at least ten daily records per month (Fig. 2); pH and hardness was recorded opportunistically in the aquarium (values remained within ranges in table I). All individuals were re-weighed and measured, twelve months after their initial weighing and measuring.

Maximum daily ration

Experience with feeding *G. polyuranodon* in the growth trial revealed that if this species is satiated it rarely feeds again for about 24 hours, allowing for a single meal to be used for estimating maximum daily ration. Maximum daily ration was quantified by recording wet weight of individu-

Figure 1. – **A**: Rainforest stream where *Gymnothorax polyuranodon* was collected; **B**: 1200-litre aquarium in which morays were housed. **C**: Individual receiving antibiotic prior to (**D**) measuring total length and (**E**) weighing. **F**: Small, recurved maxillary and vomerine teeth. Moray feeding on (**G**) fish, (**H**) earth worm and (**I**) prawn. **J**: Individuals occasionally bit congeners, particularly immediately posterior of the gill cover or on the nape. **K**: Teeth marks, usually healed rapidly. **L**: Individuals often rested together and generally coexisted without aggression.

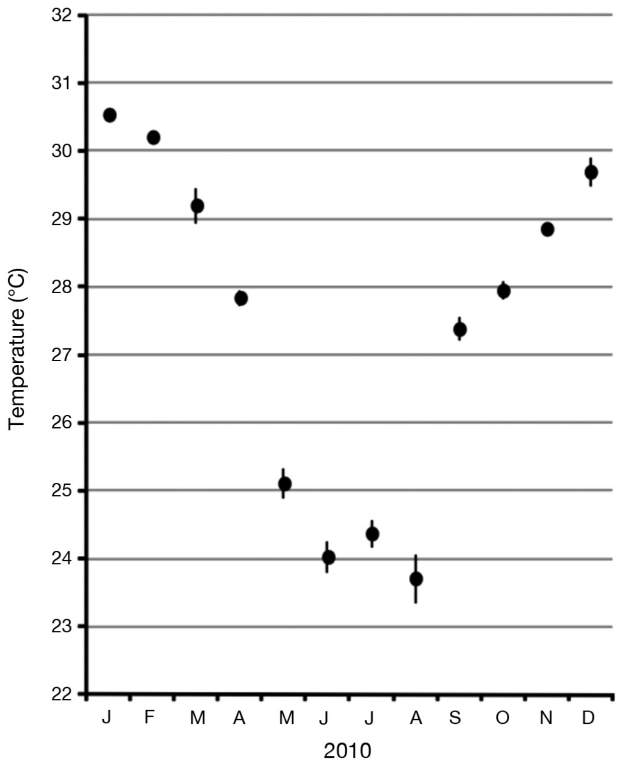

Figure 2. – Mean (± standard error) monthly water temperature in the aquarium in 2010.

al prey items (worms, prawns or fish) and the time (to the nearest minute) at which individual morays consumed these prey. A one-hour feeding period (termed an ‘offering’) was achieved on 12 occasions in the five weeks following completion of the growth trial, with maximum daily ration per individual based on the largest meal consumed during these 12 offerings. The feeding trial to obtain daily ration estimates was discontinued when all four individuals resumed feeding to satiation based on previous experience with feeding these animals at optimum temperatures. During summer months (December to February), feeding was limited to days when low water temperatures prevailed since the species appears to prefer feeding at water temperatures below about 28°C and usually refused to feed above 30°C.

RESULTS

Four *G. polyuranodon* individuals grew substantially during one year in a freshwater aquarium, ranging from a minimum increase of 21.0 cm TL and 2.4 times body mass to 26.5 cm TL and 3.9 times body mass (Tab. II). Maximum daily ration ranged from 3.5% to 4.6% of body weight (Tab. II), with minimum values corresponding to the largest individual consuming noticeably smaller meal sizes over the warmest period of the year (November 2010-March 2011;

Table I. – Temperature in the aquarium and water quality of Mareeba town water supply in 2010 (all data except temperature courtesy of Tablelands Regional Council Mareeba Water Treatment Plant).

Variable	Range
Temperature (°C)	19.9-31.0
pH	6.37-8.19
Turbidity (NTU)	< 1
Conductance (µS)	105-221
Ca hardness (mg/L)	14-45
Total hardness (mg/L)	27-60

Fig. 2) relative to what it was capable of during cooler periods. Indeed, with the exception of Individual-C, all individuals fed less frequently and usually not to satiation during warmer periods.

All individuals fed regularly throughout most of 2010 (although not during the daily ration trial, Tab. II). Inter-individual variation in feeding behaviour was apparent, with Individual-C substantially more active and was the only moray that consistently fed from the water surface and regularly swam in the water column. By contrast, Individual-A was the most recluse, was rarely active except at feeding time, and was never seen rising to the surface even to feed. Individuals B and D were intermediate between these extremes.

Multiple *G. polyuranodon* coexisted generally without conflict, with individuals commonly seen to rest and sleep in close contact or proximity to one another (Fig. 1L). Rare observations of intraspecific aggression, involved biting (Fig. 1J) usually with the largest moray, Individual-D, being the aggressor. Biting was usually based on contact immediately posterior of the head including to the nape, opercula region and gular (Fig. 1J, K; Fig. 3). However, the resultant bite marks healed rapidly (within 48 hours) via shedding of mucous and or the local epidermis.

DISCUSSION

Whilst *Gymnothorax polyuranodon* has been assumed to be euryhaline (Monkes, 2006), the current study demonstrates that this species is capable of surviving and growing substantially in freshwater. This finding combined with an increasing number of exclusively riverine based observations of adult phase *G. polyuranodon* in the field (Allen, 1991; Böhlke and McCosker, 2001; Marquet *et al.*, 2003; Jenkins *et al.*, 2009; Ebner *et al.*, 2011, 2016) lends significant support to the idea that *G. polyuranodon* may actually be a long-term riverine inhabitant in the adult phase. Adult and particularly early post-elver stage *G. polyuranodon* have been recorded from mildly brackish conditions in tropical Australian Rivers (≤ 4 ppt. salt) (Ebner *et al.*, 2011), and

Table II. – Growth of *Gymnothorax polyuranodon* from 25 January 2010 until 25 January 2011 in a freshwater aquarium, and mass of prey consumed by individuals offered twelve opportunities to feed to satiation from 29 January 2011 until 8 March 2011.

	Individual A	Individual B	Individual C	Individual D
Total length (TL, mm)				
Starting	630	650	700	735
Finishing	895	870	930	950
Increase	265	220	230	215
Finishing TL relative to staring TL (%)	142	134	133	129
Body mass (g)				
Starting	190	154	332	338
Finishing	742	502	886	1043
Increase	552	348	554	705
Finishing relative to starting mass (%)	391	326	267	309
Maximum daily ration (g)				
Prey intake (29 Jan.-8 Mar. 2011)				
Fish	3.3	8.9	134.9	17.0
Prawns	46.4	11.9	53.6	62.6
Worms	39.2	38.5	79.6	2.2
Total	88.9	59.3	268.1	81.8
Maximum daily ration	27.5	20.8	41.4	37.0
Maximum daily ration (% of body mass)	3.7	4.1	4.6	3.5
Water temperature (°C)	27.8	28.5	28.5	29.2

preliminary otolith microchemistry work points towards a freshwater adult phase. Nevertheless, the breeding ecology and larval habitat of this species remains unknown. Such knowledge gaps should be addressed, perhaps through application of acoustic tracking, genetic analyses, otolith microchemistry, larval trapping (Ebner *et al*., 2011) or salinity tolerance trials. The latter might include testing sperm motility in relation to salinity.

The potential ramifications of a muraenid in freshwater ecosystems from the perspective of food web dynamics and structuring of fish and invertebrate assemblages is also worthy of research attention. Why has the ecology of *G. polyuranodon* been overlooked in the context of freshwater ecosystems? A lack of attention to this aspect of study is surprising given the large body size of this species; however, it is understandable given the elusive nature of this eel and its distribution primarily being centred on remote Pacific Islands. *Gymnothorax polyuranodon* mainly fed on prepared foods in the current study and was largely disinterested in hunting live fishes. However, this may have been an artefact of the functional swimming mode of small fish species co-inhabiting the aquarium. *Gymnothorax polyuranodon* may simply be adept at feeding on the occupants of interstitial spaces rather than being a water column specialists (as most of the potential prey fishes (*M. splendida*, *C. rhombosomoides, H. compressa, C. stercusmuscarum*) present in this captive study inhabit the water column). The few individuals of *Glossogobius illimis* (a benthic species) resident in the aquarium in the current study were relatively large-bodied in terms of gobies (> 10 cm TL) and were able to evade the morays for about six months. Presumably *G. polyuranodon* eventually captured these *G. illimis*. The natural diet of *G. polyuranodon* remains unknown but may well comprise caridean shrimps (*e.g.* Atyidae and *Macrobrachium* spp.) and gobioids, since these benthic taxa are major constituents of the fauna in insular streams of tropical Indo-Pacific Islands including continental Australia (Johnson, 1963; Keith, 2003; Thuesen *et al*., 2011).

Rapid growth of *G. polyuranodon* was observed in the current study. Water temperature ranged from 19.1-31.0°C in the current study and this is comparable with likely field scenarios in the Australian Wet Tropics (*e.g.* the annual thermal range is approximately 16-31.0°C in the lower Mossman River: https://water-monitoring.information.qld.gov.au/). Graynoth and Taylor (2000) noted that growth of captive freshwater eels (*Anguilla* spp.) fed regularly on a high quality diet can be substantially greater than growth of wild eels, serving as a reminder that the results of the current study may not simulate natural growth rates. However, the growth of *G. polyuranodon* or indeed morays in general, under field conditions, remains largely unknown. Back-calculation of natural growth rate partly from ageing otoliths may be possible in time, although, this is currently inhibited by the lack of available specimens and the ethical and conservation issues associated with sacrificing individuals of a potentially rare species.

Individual differences in growth rate were observed in the current study. Substantial among-individual differences in growth rate of freshwater eels (*Anguilla* spp.) have been recorded under field and captive conditions (Knights, 1987; Holmgren, 1996; Walsh *et al*., 2006). In captivity, individual variability in growth has been partly attributed to the formation of dominance hierarchies (Knights, 1987; Holmgren, 1996). In the current study Individual-D was the dominant moray in the aquarium, occasionally being observed chasing or biting other individuals. However, this aggression usually occurred outside of feeding time and rarely led to other individuals being excluded from food. More likely the differential growth of the four morays observed in the current study

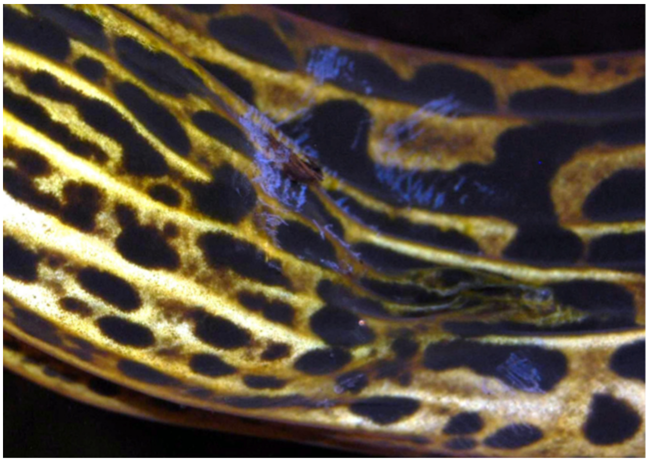

Figure 3. – A close up of the fine abrasions resulting from intraspecific biting of *Gymnothorax polyuranodon* on and immediately posterior of the opercula region.

was driven by individual differences in activity level during non-feeding periods and to a lesser extent net food consumption (see behavioural descriptions in results).

The maximum daily ration of morays has received modest attention. Indications from the current study are that adult *G. polyuranodon* are capable of consuming a meal size in the order of 3.5% to 4.6% of body weight (Tab. II). This may represent a slight underestimate, as (in hindsight) summer was not the optimum time to be quantifying maximum feeding rates of *G. polyuranodon*. Specifically, individuals fed sporadically in summer and consequently because stomach capacity can be adaptive in relation to meal size and frequency (Heinsbroek *et al.*, 2008). Young and Winn (2003) provide a field-based record of *Gymnothorax vicinus* (721 mm TL) with a 77.9 g squirrelfish, *Holocentrus ascensionis*, in its stomach, equating to 14.1 % of the predators body weight. Young and Winn (2003) also estimated that a digested squirrelfish that would have been of comparable size to that in the previous example was found in the stomach of a 669 mm TL *Gymnothorax moringa*. Clearly, these two marine morays are top predators capable of feeding on substantially larger prey than *Gymnothorax polyuranodon*. A more comprehensive understanding of the feeding ecology of muraenids could be obtained by ascertaining the maximum meal size and daily ration of other morays, including durophagous species (see Mehta, 2009; Reece *et al.*, 2010) that presumably feed on relatively small prey items and have small overall meal sizes (similar to or less than that achieved by *G. polyuranodon*).

There was a degree of caution associated with stocking an aquarium with multiple individuals of *G. polyuranodon* (and indeed a fifth comparatively small individual was not held with the others for fear of adverse intraspecific aggression and even cannibalism). Young and Winn (2003) reported adult cannibalism on juveniles in two species of marine morays (*Gymnothorax moringa* and *G. vicinus*). The relatively small teeth and small gape of *G. polyuranodon* relative to its body size preclude cannibalism of adults by adults. Presumably the oral jaws and dentition of this species are adapted for hunting invertebrates and small fishes. However, the general compatibility of adults in an aquarium (this study) bodes well for attempting to spawn *G. polyuranodon* in captivity. This presents an unusual opportunity, since many moray species are kept in solitude to avoid intra- and inter-specific aggression (Purser, 2005). However, success in breeding this species in captivity may be contingent on developing knowledge of its habitat use in the wild and by paying particular attention to its life-cycle in relation to salinity.

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